

Chapter 7

Biogeography, rarity and endemism in *Cineraria* (Asteraceae).

Abstract

The biogeography of the afromontane genus *Cineraria* (Asteraceae) is assessed and discussed with reference to its distribution range and centres of diversity and endemism. Plotting the numbers of species per degree square for southern Africa reveals that the centre of diversity for *Cineraria* is in the KwaZulu-Natal Midlands, part of the Maputaland-Pondoland Centre of Endemism, with a secondary centre of diversity in the Albany Centre of the Eastern Cape. The main affinity of *Cineraria* is afromontane (to afroalpine) within various centres of diversity and endemism. Fifteen species endemic to specific mountains or regions of endemism and five near-endemics are identified. Rare species are identified and classified/categorised according to Rabinowitz's criteria of geographic range, habitat specificity and local population size. Rare species (in the sense of low abundance, restricted range and high habitat specificity) number at eleven, however only six or seven are considered under threat as indicated by IUCN Red Data Criteria - but a number are data deficient. Causes of rarity in *Cineraria* are linked to narrow habitat specificity, particularly soil or rock type and/or altitudinal range.

Introduction

Cineraria L. of the Senecioneae (Asteraceae) comprises 35 species and is essentially an African genus, with one species (*C. anampoza*) endemic to Madagascar and another (*C. abyssinica*) extending from Ethiopia into the mountains of Yemen and Saudi Arabia (see Table 1 for a list of the species, including author citations). *Cineraria* is intrinsically an afromontane (to afroalpine) genus, but descends to sea level in the Western Cape (*C. geifolia* and *C. humifusa*), thereby exhibiting an 'African track' distribution pattern (Linder *et al.*, 1992). *Cineraria* shows a distribution pattern similar to a number of other genera in the Asteraceae, viz. *Athrixia* Ker Gawl., *Felicia* Cass., *Osteospermum* L., *Pentzia* Thunb., *Stoebe* L. and *Ursinia* Gaertn. (Koekemoer, 1996).

The majority of species of *Cineraria* occur in southern Africa, with only a few extending into the equatorial zone and the northern hemisphere. Most of the species are fairly limited in their distribution and many are associated with recognised areas of endemism. The most widespread species is *Cineraria deltoidea* (including plants previously known as *C. grandiflora* Vatke), which occurs throughout the mountains of the Rift Valley of Africa, including the high plateau regions of Malawi (Nyika, Zomba, Mlanje and mountains near Blantyre), the eastern highlands of Zimbabwe, as well as in the Soutpansberg, KwaZulu-Natal Midlands and on forest margins in the Eastern Cape in South Africa. Widespread species

within South Africa include *C. aspera*, *C. erodioides* and *C. lyratiformis*, all of which also occur at high altitude in Lesotho. *Cineraria aspera* and *C. lyratiformis* are somewhat weedy/pioneer species, often growing in disturbed areas. *Cineraria abyssinica* has also been noted to grow along the edge of fields and near roadsides in Ethiopia, and *C. anampoza* (from Madagascar) has been described as a “weedy perennial” [Phillipson 1604 (MO, WAG)]. Most other species of *Cineraria* have quite specific habitat requirements.

A number of species in *Cineraria* are either rare and/or endemic to specific regions, and a few have been categorised as endangered, vulnerable, near threatened or data deficient according to the IUCN (2001) criteria (Scott-Shaw, 1999; Pfab & Victor, 2002; Cron, 2005: Chapter 6.). For conservation purposes, it would be useful to identify rare and endemic species in *Cineraria* and possible causes for their rarity.

The aims of this paper are to (i) map the distribution of *Cineraria* in Africa, (ii) identify centres of diversity for *Cineraria*, and analyse its distribution in relation to currently defined phytogeographic units, (iii) identify rare and endemic species and relate these to centres of endemism, and (iv) identify possible causes of rarity in the genus.

Materials and Methods

Distributional data were obtained for the 35 species of *Cineraria* as described in Chapter 6 from specimens borrowed from the following herbaria and/or examined on site: BM, BOL, BR, COI, E, EA, G-DC, GRA, J, K, LISC, MO, NBG, NH, NU, P, PRE, PRU, S, SAM, SRGH, TCD, UPS, US, WAG, Z. Information concerning ecology and habitat was compiled from personal observations in the field and from notes on herbarium specimen labels.

The number of species of *Cineraria* in each country was counted and mapped. The number of species per degree square/cell was counted and mapped for southern Africa and the distribution of the six species occurring in the regions of Africa north of 16° S was plotted. In addition, the number of one degree squares and quarter degree squares occupied by each species was counted using the maps produced using Mappit Version 2 (Arnold & Oliver, 1996) from the distribution data gathered (see Chapter 6).

The rarity of each species was assessed using the criteria proposed by Rabinowitz (1981; 1986): geographic range, habitat specificity and local population size. Each of these attributes is dichotomised in an 8-celled block. Large distributions in the geographical range were interpreted as distribution areas with a longest diameter of more than 200 km (Linder, 1995; Schutte *et al.*, 1995). Habitat specificity refers mainly to soil type (or geological formation) and altitude, where a narrow specificity was coded for a species that occurs on only one soil type (Linder, 1995) and/or has an altitude range of 500 m or less (Schutte *et al.*, 1995). Small

populations are those with fewer than 50 individuals, while large populations have more than 50 individuals (Linder, 1995). Species were coded as having a large population if somewhere a population of more than 50 individuals is known to exist or is indicated as being e.g. “locally abundant”, “common”, “frequent” on herbarium labels. Population size is difficult to code for *Cineraria* as plants tend to grow in patches of suitable habitat - often amongst boulders or rocks (e.g. *C. decipiens*, *C. pulchra*, *C. austrotransvaalensis*) or in drainage lines at the base of cliffs (e.g. *C. mollis*) or scattered in the grassland (e.g. *C. geraniifolia*, *C. vagans*).

A species was considered to be endemic to a region if it occurred only in that region or specific Centre of Endemism and near-endemic if the species occurs (with limited distribution) in an adjacent region outside of the area of reference. Recognised Centres of Endemism and/or Centres of Diversity are/were referred to using Van Wyk & Smith (2001) and Beentjie *et al.* (1994).

Results

The majority of species (32/35; 91%) of *Cineraria* occur in southern and subtropical Africa (including southern Angola and Malawi) and 27 in South Africa (Figure 1). Seventeen species occur only in South Africa with another four occurring in Lesotho as well; one species (*C. decipiens*) also occurs in Swaziland and another species is endemic to the Ngwenya Hills in Swaziland, bringing to 23 the species in these three southern-most countries of Africa. Three species (*C. alchemilloides*, *C. canescens* and *C. vallis-pacis*) occur in Namibia and the Northern and Western Cape provinces of South Africa.

The number of species of *Cineraria* occurring in each degree square of southern Africa is presented in Figure 2, while the numbers of degrees and quarter degrees a species occupies is summarised in Table 1, along with the distributional, ecological and associated centres of endemism. The distribution of the six species occurring in Africa north of 16° S is shown in Figure 3. *Cineraria deltoidea* and *C. abyssinica* co-occur in only four degree squares in Ethiopia, and *C. deltoidea* and *C. foliosa* occur together in the southern highlands of Tanzania; no other species are recorded as co-occurring (Figure 3). (Note: Distributions of *C. abyssinica* on the Arabian Peninsula and *C. anampoza* in Madagascar are not shown here.) The Rabinowitz rarity values for each species are given in Table 2 and the rarity of each species is summarized in Table 1.



Figure 1. Distribution of *Cineraria* in Africa and south-west Asia, indicating numbers of species in each country. (DRC = Democratic Republic of Congo; L = Lesotho; Moz = Mozambique; Sw = Swaziland; U = Uganda; Zim = Zimbabwe.)

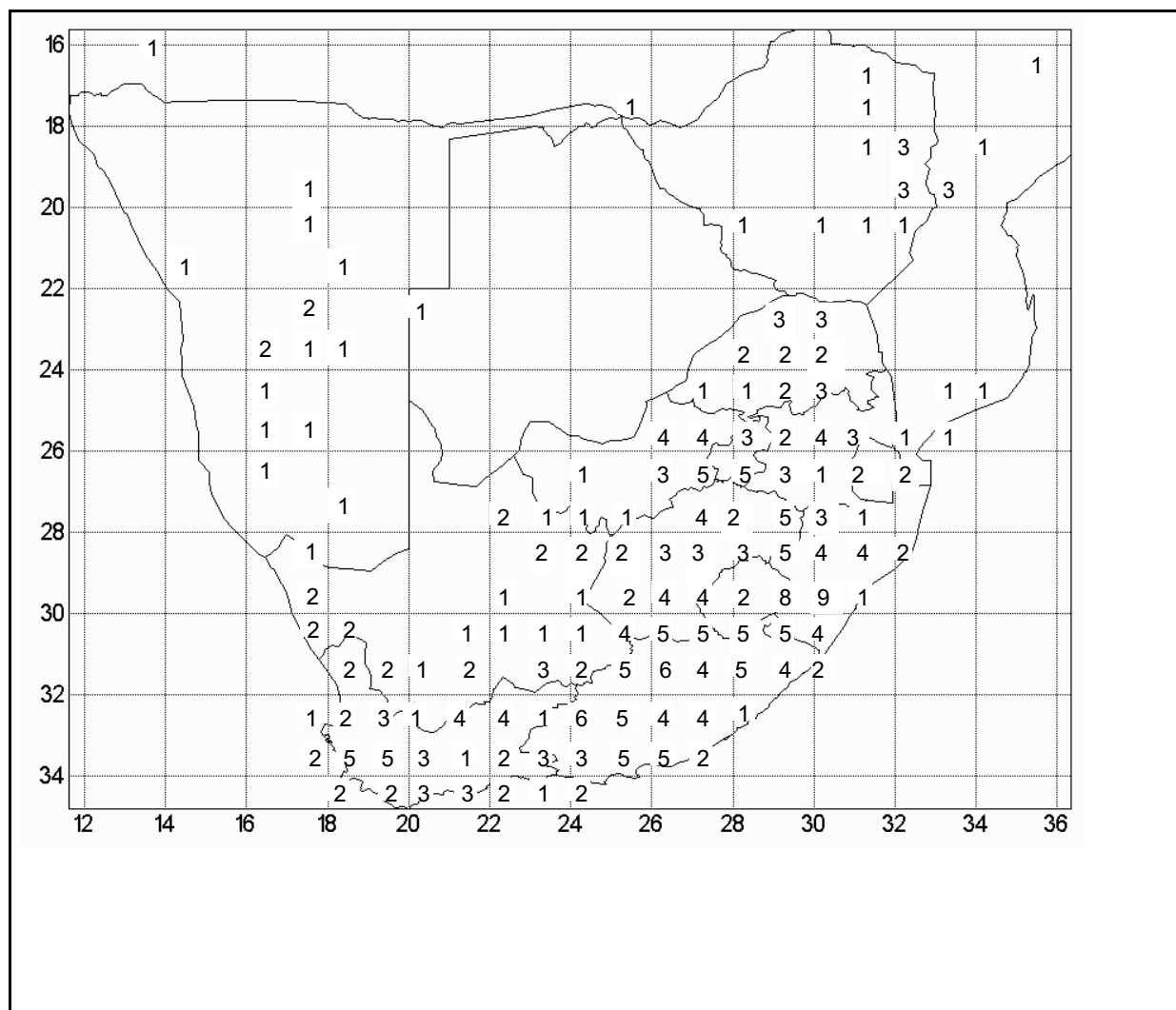


Figure 2. Number of species of *Cineraria* occurring in each degree square in southern Africa.

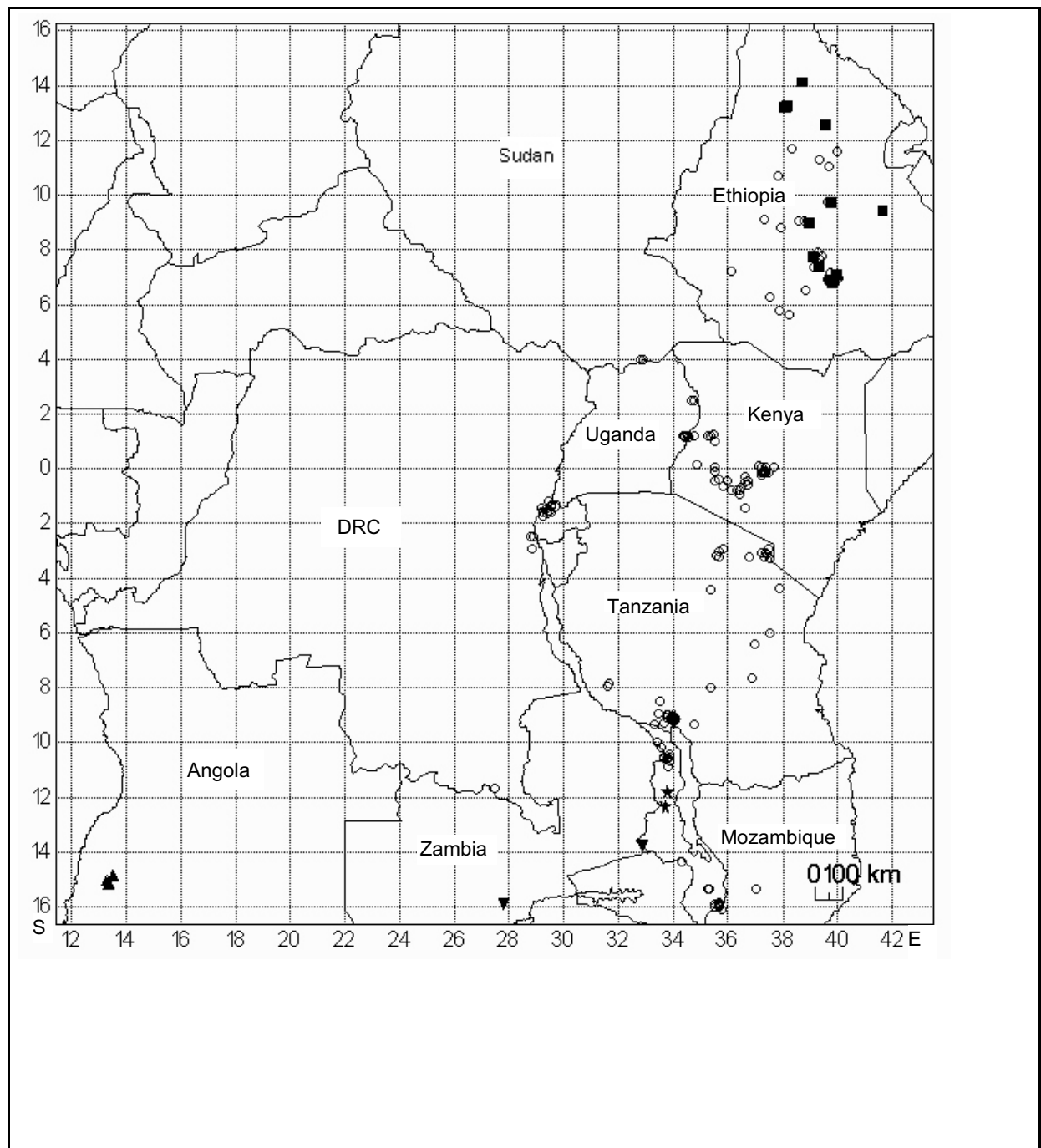


Figure 3. Distribution of the six species of *Cineraria* occurring north of 16° S: ○ *C. deltoidea*, ■ *C. abyssinica*, ◇ *C. foliosa*, ★ (star) *C. magnicephala*, ▲ *C. huilensis*, ▼ *C. mazoensis*.

Table 1. Ecology, Distribution and Rarity of the species of *Cineraria*.

Species of <i>Cineraria</i> + authorities?	#	#	Distribution ^a	Popln size	Altitude Range (m)	Soil Types ^b	Centres of Endemism ^c	Rarity ^d	IUCN Category ^e
abyssinica Sch. Bip. ex A. Rich.	15	23	Ethiopia, Eritrea, Yemen, Saudi Arabia	L	2300 – 4100	LS + loam	Bale Mts, Simen Mts	N	DD
albicans N.E.Br.	9	16	KZN, EC	L	170 – 2600	NGS + MFS	Albany, DA	N	LC
alchemilloides DC.	14	19	NC, WC, Namibia	S	800 – 1750	Q, G	Brandberg + CFR?	** (N/WC); * (Namibia)	DD; LC
anampoza (Baker) Baker	6	10	Madagascar	L?	1200 – 2600	Q, clay, laterites	(Madagascar)	N?	DD
aspera Thunb.	49	99	SA, Lesotho	L	1400 – 2600	Q, D	Albany, DA	N	LC
atriplicifolia DC.	3	7	KZN	S	30 – 1200	NGS	KZN Midlands in MPR	**	NT
austrotransvaalensis Cron	5	9	Gauteng, NW, MP	S	1400 – 1700	Q, D		*	VUB2ab(iii)
canescens Wendl. ex Link	7	12	NC, WC, Namibia	S	570 – 1600 (–2200)	G	Khamiesberg in CFR	*	DD
cyanomontana Cron	1	1	Blouberg (L)	S	1700 – 2000	Q	SC (Blouberg)	***	ENB1a+2aD
decipiens Harv.	9	11	KZN, Swaziland	S	100 – 1150	MFS, G, NGS?	MPR	*	LC
deltoidea Sond.	62	220	Eth, EA, Malawi, L, MP?, KZN, Zambia, Zimbabwe	L	500 – 4300	NGS, Dol, B	Bale Mts, Imatong, Mt Kenya, Mt Mlanje, Ch, SC, KZN Midlands in MPR	N	LC
dryogeton Cron	1	1	KZN	S	300 – 400	MFS	Pondoland (MPR)	***	ENB2ab(iii)D
erodioides DC.	38	101	SA, Lesotho	L	100 – 3300	B, NGS, Q?	DA, Albany, SC, W	N	LC
erosa (Thunb.) Willd.	9	23	WC, NC	S	300 – 1750	G, CSS	CFR	*	LC
foliosa O.Hoffm.	1	1	Kitulo, Tanzania	S	2700		SH Tanzania	***	DD/ CRB1ab(iii)+ 2ab (iii)
geifolia (L.) L.	6	28	WC	L	10 – 500	Coastal sands	CFR	*	LC
geraniifolia DC.	21	46	EC, KZN, MP	S	(0 –) 1300 – 2550	B, Dol, NGS?	DA, Albany	*	LC
glandulosa Cron	3	5	KZN	S	630 – 1800	NGS	KZN Midlands in MPR	***	NT
grandibracteata Hilliard	4	9	KZN, EC	S	450 – 1900	Dol	KZN Midlands in MPR	*	LC
huilensis Cron	2	5	Angola	S?	1700 – 2400	Q/G?	Huila	**?	DD
humifusa L' Hér.	2	2	WC	S	ca. 30	G	CFR?	***	DD
lobata L' Hér.	29	64	WC, EC, NC, L	L	10 – 1800	CSS, Q, G	CFR, Albany, SC	N	LC
longipes S.Moore	2	5	Gauteng	S	1500 – 1850	B		***	ENB1ab(i,ii,iii,iv,v)+ 2ab(i,ii,iii,iv,v)+C1+2a(i)
lyratiformis Cron	35	88	SA, Lesotho	L	1250 – 2450	Q, Dol	Midlands in MPR, Albany, DA	N	LC
magnicephala Cron	2	2	Malawi	S	1900 – 2030	Q?	?	***	DD
mazoensis S.Moore	12	14	Zimbabwe, Zambia, M	S	1100 – 1650 (–1905)	Q, G		*	DD

Species of <i>Cineraria</i> + authorities?	# 1DS	# QDS	Distribution ^a	Popln size	Altitude Range (m)	Soil Types ^b	Centres of Endemism ^c	Rarity ^d	IUCN Category ^e
<i>mollis</i> E.Mey. ex DC.	19	33	WC, EC, NC, Lesotho	L	1600 – 2550	B, Dol, NGS	DA	N	LC
<i>ngwenyensis</i> Cron	1	1	Swaziland	S	1500 – 1700	Q	Barberton	***	VUB1a+2aD1+2
<i>parvifolia</i> Burt Davy	11	17	Gauteng, NW, L, MP	L	1250 – 1600 (–2000)	Q, sandy loams		N	LC (NT in Gauteng?)
<i>pinnata</i> O.Hoffm.	5	8	KZN, Moz	L	20 – 70	Coastal sands	Maputaland in MPR	*	DD (Scott-Shaw, 1999)
<i>platycarpa</i> DC.	14	31	WC, EC	L	20 – 900	Bokkeveld & Ecca shales	Little Karoo (in CFR)	*	LC/NT?
<i>pulchra</i> Cron	4	7	Zimbabwe, Moz	L	1700 – 2540	Q, G	Chimanimani-Nyanga	N	LC
<i>saxifraga</i> DC.	6	18	EC, (FS)	L	400 – 1000	Q	Albany	*	LC
<i>vagans</i> Hilliard	1	2	EC	S	1380 – 1750	D	Albany	***	ENB2aC1
<i>vallis-pacis</i> Dinter ex Merxm.	10	23	NC, Namibia	L	1140 – 2000	D (TSG), Kalahari sands? +?	GWC	N	LC

^a Distribution: Eth = Ethiopia, EC = Eastern Cape, FS = Free State, KZN = KwaZulu-Natal, L = Limpopo Province, Moz = Mozambique, MP = Mpumalanga, NC = Northern Cape, SA = South Africa (widespread), WC = Western Cape.

^b Soil types/geological formations: B= basalt, CSS = Cape Supergroup Sandstone, D = dolomite, Dol = dolerite, G = granite, LS = limestone, MFS = Msikaba Formation Sandstone, NGS = Natal group Sandstone, Q = quartzite.

^cCentres of Endemism/Floristic Regions: CFR = Cape Floristic Region, DA = Drakensberg Alpine Centre KZN = KwaZulu-Natal, GWC = Griqualand West Centre, MPR = Maputaland-Pondoland Region, SC = Soutpansberg Centre.

^dRarity: N = common, not rare; * = intermediate; ** = Fairly rare; *** = Rare.

^eIUCN Red Data Categories: DD = data deficient; EN = endangered; LC = least concern; VU = vulnerable.

Table 2. Rabinowitz (1981, 1986) rarity values for the species of *Cineraria*.

Geographical Distribution				
	Large		Small	
Habitat Specificity	Wide	Narrow	Wide	Narrow
Somewhere Large Populations	<i>abyssinica</i>	<i>geifolia</i> (alt.)		
	<i>albicans</i>	<i>pinnata</i>		
	<i>anampoza</i>	<i>saxifraga</i> (geol)		
	<i>aspera</i>	<i>platycarpa</i> (geol)		
	<i>deltoidea</i>			
	<i>erodioides</i>			
	<i>lobata</i>			
	<i>lyratiformis</i>			
	<i>mollis</i>			
	<i>parvifolia</i>			
	<i>pulchra</i>			
	<i>vallis-pacis</i>			
All Small Populations	<i>alchemilloides</i>	<i>canescens</i> (geol)		<i>atriplicifolia</i> (geol)
	<i>austrotransvaalensis</i>	<i>grandibracteata</i> (alt.)		<i>cyanomontana</i>
	<i>decipiens</i>			<i>dryogeton</i>
	<i>erosa</i>			<i>foliosa</i>
	<i>geraniifolia</i>			<i>glandulosa</i>
	<i>mazoensis</i>			<i>huilensis</i> (geol?)
				<i>humifusa</i>
				<i>longipes</i>
				<i>magnicephala</i>
				<i>ngwenyensis</i>
				<i>vagans</i>

Discussion

Centres of diversity and centres of endemism for Cineraria

Plant endemism in southern Africa south of the Kunene, Okavango and Limpopo Rivers is 80% (Cowling & Hilton-Taylor, 1994). This is comparable with what is seen in *Cineraria*, where 26 of the 35 (74%) species occur here (Figure 1, Table 1). If *C. pinnata*, which occurs

in northern KwaZulu-Natal and southern Mozambique, is included, the percentage endemism increases to 77.

The centre of diversity for *Cineraria* is the KwaZulu-Natal Midlands (grid squares 2929 and 2930) with eight and nine species respectively (Figure 2), with 34% (12/35) of the species occurring in the province as a whole. This centre is part of the larger Maputaland-Pondoland Phytogeographic Region (Van Wyk & Smith, 2001) and is dissected by river gorges with grasslands predominating, but with pockets of forest on the mountains or hills. The Midlands merge into the foothills of the Drakensberg escarpment and the altitudinal range is considerable (600–1500 m). All these factors contribute to a varied landscape that can accommodate a wide diversity of plants.

The Asteraceae outnumber any other family of flowering plants in KwaZulu-Natal: 551 indigenous species in 113 genera, with 30% endemic to the province (Hilliard, 1978). Hilliard (1978) described two minor centres of endemism in Natal, one associated with the Natal Group and Msikaba Formation sandstones (where about 4% of the Asteraceae endemic to KwaZulu-Natal occur); the other on the sandy Maputaland coastal plain. *Cineraria* occurs in both these centres, with *C. dryogeton*, *C. glandulosa* and *C. atriplicifolia* endemic to the sandstones, and *C. pinnata* endemic to the Maputaland coastal plains which extend into southern Mozambique. *Cineraria albicans* is a near-endemic to the sandstones, also occurring at high altitude in the southern Drakensberg in the Eastern Cape. *Cineraria grandibracteata* is also a near-endemic to the KwaZulu-Natal Midlands as it occurs in the adjacent mountain peaks of the EC, but mainly associated with dolerite.

The Eastern Cape follows as the next most diverse area, notably grid squares 3126 and 3224 with six species of *Cineraria* occurring in each. These cells are part of the Albany Centre of Endemism, long recognised as an important centre of species diversity and endemism (Croizat, 1965; Nordenstam, 1969; Cowling & Hilton-Taylor, 1994; Beentjie *et al.*, 1994; Phillipson, 1995; Van Wyk & Smith, 2001; Victor & Dold, 2003). No fewer than five of White's (1983) phytochoria converge in this region, namely, the Cape Region, the Karoo-Namib Region, the Maputaland (Tongaland)-Pondoland Regional Mosaic, the Afromontane Region and the Kalahari Highveld Regional Transition Zone. This creates a diverse mosaic of floristic elements and vegetation types. Fifteen percent of the approximately 4000 vascular plant species occurring in the region are endemic or near-endemic to this centre (Van Wyk & Smith, 2001), which boasts almost one third of Acocks' (1953) 70 veld types (Victor & Dold, 2003).

The Albany Centre of endemism is topographically very variable, extending from sea-level in the south and southeast to about 2100 m in the northwest and 1500 m in the northeast (Van Wyk & Smith, 2001). The area below the Great Escarpment of the Winterberg (2360 m) is dissected by numerous rivers, and rainfall is bimodal with maxima in spring and

autumn. Geologically it is also very variable with Table Mountain Group sandstones in the mountains south and west of Uitenhage and Port Elizabeth; Bokkeveld Group shales in the valleys and low hills and Witteberg Group quartzite and sandstone in e.g. the Suurberge, although much of the area is underlain by the Karoo Supergroup (Van Wyk & Smith, 2001). *Cineraria saxifraga* and *C. vagans* are endemic to this region, and it is the area where at least three species (viz. *C. erodioides*, *C. lobata* and *C. geraniifolia*) show a great amount of phenotypic variation. A subspecies of *C. lobata* (ssp. *platyptera*) has been recognised in the region (Chapters 4 and 6). Hybridisation is possibly taking place with intermediates between *C. lobata* and/or *C. erodioides* and *C. geraniifolia* occurring in this region.

Afromontane Centre of Endemism

Most species of *Cineraria* are afromontane in their affinity, even though they may occur in other centres of diversity and/or endemism. The Afromontane Region itself is described by White (1978; 1983) as an archipelago-like centre of endemism, with most of the ‘islands’ of volcanic origin, though of different ages. Most of the afromontane communities in the tropics are above 2000 m, but they may occur at lower altitudes (e.g. 1200 m in the West Usambara Mountains in Tanzania) and occur only a few hundred metres above sea-level in the Cape, where latitude compensates for altitude (White, 1983). These montane areas are scattered “islands” of a distinctive flora surrounded by other vegetation types (Beentje *et al.*, 1994). As noted previously, only *C. deltoidea* extends almost the full length of the eastern highlands of Africa, where it occurs between 1600 and 4300 m in East Africa, and from 200 to 1700 m in KwaZulu-Natal and the Port St Johns area of the Eastern Cape. *Cineraria abyssinica* extends from the afromontane regions of Ethiopia into the Afromontane Regional Centre of Endemism in south-western Arabia, a small region that is floristically extremely impoverished compared to the afromontane regions of Africa (Boulos *et al.*, 1994). In Ethiopia, *C. abyssinica* and *C. deltoidea* both occur in the Bale Mountains and *C. abyssinica* also occurs in the Simén Mountains, both important centres of plant diversity (Beentje *et al.*, 1994). *Cineraria deltoidea* also grows on the Imatong Mountains in southern Sudan, Mount Elgon and Mount Kenya, all recognised as centres of plant diversity (Beentje *et al.*, 1994).

Three fairly unknown species occur in diverse parts of this afromontane archipelago of Africa. *Cineraria foliosa* occurs on the Kitulo Plateau in the Kipengere Range of the southern highlands of Tanzania, a recently proclaimed conservation area, famous for its large number of endemic terrestrial orchids (Davenport & Bytebier, 2004). It is known only from the type specimen, most likely collected on Mount Mtorwi at 2700 m. *Cineraria magnicephala* is known from two mountain peaks in central Malawi, and some unusual forms of *C. cf. deltoidea* occur on Mount Mulanje, another noted centre of diversity and endemism (Beentje *et al.*, 1994). *Cineraria huilensis* appears to be endemic to the Huila

district in Angola, an important region of endemism (Brenan, 1978) and also part of the Afromontane Regional Centre of Endemism (Huntley & Matos, 1994).

Cineraria pulchra is endemic to the Chimanimani-Nyanga Centre, where it occurs in the mist belt at altitudes between 1700 and 2540 m, growing amongst rocks for protection against fire. The Chimanimani range is characterised by quartzite rocks, sandy soils, and poor nutrients, but granites as well as sedimentary shales and siltstones of the Umkondo Group occur in the Nyanga region (Stagman, 1978). It is a meeting ground for Afromontane floristic elements from both north and south, and is characterised by high levels of grassland endemism, with most of the endemics confined to the quartzite-derived soils (Wild, 1964).

Other centres of endemism in southern Africa

Other Centres of Endemism in southern Africa in which *Cineraria* occurs are: (i) the Cape Floral Region (CFR), (ii) the Little Karoo, (iii) the Drakensberg Alpine Centre, (iv) the Soutpansberg Centre, (v) Wolkberg Centre and (vi) the Barberton Centre.

The Cape Floristic Region (CFR) extends from near Vanrhynsdorp and Nieuwoudtville (Bokkeveld Mountains) in the west down to Cape Town and eastwards to Grahamstown, and is dominated by the sub-parallel ranges of the Cape Fold Belt mountains. The CFR comprises a number of local centres (and subcentres) of endemism (Goldblatt and Manning, 2002), including the Kamiesberg Centre (according to Van Wyk & Smith, 2001), characterised by massive granitic domes among granite hills and sandy plains. *Cineraria canescens* is a near endemic to this region and is very similar to and apparently closely related to *C. erosa*, which occurs in the mountains near Paarl, Worcester and Montagu. These two species may be evidence of speciation due to isolation resulting from vicariance as the climate became drier, leaving high-altitude refugia in the granitic hills of the Kamiesberg Centre, as suggested by Weimarck (1941).

Cineraria geifolia and *C. humifusa* are endemic to the CFR and are unusual *Cineraria* species in that both occur at sea-level: *C. geifolia* amongst dune vegetation on mainly the southern coast and *C. humifusa* on the rocks near Saldanha Bay on the west coast. A more glabrous form of *C. geifolia* occurs at higher altitude on mountain slopes adjacent to the coast, where *C. lobata* (ssp. *lobata*) also occurs.

Cineraria platycarpa is a near-endemic to the Little Karoo Region, the arid intermontane valley between the Langeberg and the Swartberg in the Western Cape that extends from about Montagu in the east to Uniondale in the west (Van Wyk & Smith, 2001). The region shows strong links with the Albany Centre in the east, with the inter-montane valleys providing migration routes. This is evident in the different forms of *C. lobata* ssp. *lobata* that occur here.

Cineraria ngwenyensis occurs on the quartzite ridges of the Ngwenya Hills in the Malolotja Nature Reserve, which falls into the Barberton Centre of Endemism, characterised by the Barberton Supergroup, a complex and unique lithostratigraphic succession of deformed volcanic and sedimentary strata. Most of the endemics are grassland endemics and many are edaphic specialists on serpentine soils, although not many in the Asteraceae (Van Wyk & Smith, 2001). Floristically it is part of the Afromontane Region and has close links with the Wolkberg Centre, where *C. erodioides* occurs on both the Mariepskop and in the Wolkberg mountains.

The Soutpansberg Centre of endemism includes the Soutpansberg, a narrow mountain range running east-west, separated in the west from the Blouberg Massif (the highest point, 2051 m) and in the northeast, Lake Fundudzi (Van Wyk & Smith, 2001). The principal rock types are sandstone and quartzite and the southern slopes much wetter than northern slopes. Fog is common at high altitude and a fynbos type vegetation is found at high altitude, especially on the Blouberg, to which *C. cyanomontana* is endemic. The wetter parts of the Centre have floristic links with the Wolkberg, the north-eastern Drakensberg and the Chimanimani-Nyanga Centre and form part of the Afromontane archipelago. *Cineraria deltoidea* occurs here, with the nearest populations in the KwaZulu-Natal Midlands to the south and the Chimanimani region to the north. *Cineraria lobata* ssp. *soutpansbergensis* and *C. erodioides* var. *tomentosa* are both endemics at the infraspecific level in *Cineraria*.

The Drakensberg Alpine Centre (over 1800 m) is recognised as a distinct floristic region by Van Wyk & Smith (2001), based on climatic considerations, not implying floristic links with the Afroalpine regions of east Africa. Alpine vegetation occurs at about 2800–3500 m and subalpine at about 1800–2800 m. The Centre shows strong floristic links with the Cape Floral region and the Afromontane Region. No endemic species of *Cineraria* occur here, but ranges of four widespread species include this centre (*C. erodioides*, *C. aspera*, *C. mollis* and *C. albicans*), and *C. lyratiformis* is found at lower altitudes. *Bolandia pedunculosa* (previously *C. albomontana* Hilliard), one of the two species of *Bolandia*, the putative sister group to *Cineraria*, also occurs here.

Cineraria vallis-pacis occurs in the Griqualand West Centre of Endemism in the Northern Cape, as proposed by Van Wyk & Smith (2001). It grows on the north-facing slopes of the low hills in reddish-brown sandy soil derived from the Ghaap Group of the Transvaal Supergroup, mainly originating from dolomite. The Kuruman and Asbestos Hills are banded ironstone, while the Postmasberg Group contains manganese and iron ore and the Olifantshoek Group is mainly composed of clastic elements (Van Wyk & Smith, 2001). The main vegetation type in the western mountains where *C. vallis-pacis* mainly occurs is Kalahari Mountain Bushveld, endemic to the centre (Low & Rebelo, 1996). *Cineraria vallis-pacis* also occurs in Highveld Savanna in the mountains around Windhoek in

Namibia, locally known as the Windhoek Bergland (Giess, 1998). It grows along the river banks, in deep sands.

Cineraria alchemilloides ssp. *namibiensis* also grows in the mountains around Windhoek, in the Waterberg to the north, and in Namaland and the Kububberge to the south, mainly on granite. It also occurs on the Brandberg, where it is unusually glabrescent and has larger capitula. The Brandberg is itself known for a number of endemic plants (Craven & Craven, 2000; Van Jaarsveld & Voigt, 2004).

A number of species are not associated with centres of endemism: *C. longipes* is endemic to Gauteng and is unusual in that it occurs on Ventersdorp Basic Lava (basalt?), not on the quartzite ridges common in the area - where *C. austrotransvaalensis* occurs. *Cineraria parvifolia* is restricted to grasslands of Gauteng, North-West and Limpopo Provinces at altitudes between 1200 and 1600 m, with a population with larger capitula at 2000 m in the Steenkampsberg in Mpumalanga.

Thus, fifteen species are endemic to specific mountains or regions of endemism: *Cineraria cyanomontana* (Blouberg, Limpopo Province), *C. longipes* (Gauteng), *C. pinnata* (Maputaland), *C. glandulosa* (KZN Midlands), *C. atriplicifolia* (KZN), *C. dryogeton* (Umtamvuna Nature Reserve, KZN), *C. ngwenyensis* (Ngwenya Hills, Swaziland), *C. vagans* (Albany Centre, Eastern Cape), *C. humifusa* (Saldanah Bay, Western Cape), *C. geifolia* (CFR, Western Cape), *C. magnacephala* (two mountain peaks in central Malawi), *C. huilensis* (Serra da Chela in Huila region of Angola), *C. pulchra* (Chimanimani-Nyanga Centre), *C. foliosa* (Kitulo Plateau, Kipengere Range, southern Tanzania), *C. anampoza* (Madagascar). Near-endemics number five: *C. saxifraga* (Albany Centre and south-eastern Free State), *C. albicans* (KwaZulu-Natal and Eastern Cape), *C. grandibracteata* (KwaZulu-Natal and Eastern Cape), *C. decipiens* (KwaZulu-Natal and Swaziland), *C. vallis-pacis* (Northern Cape and Namibia).

Rarity and causes of rarity in Cineraria

Eleven species in *Cineraria* are rare, according to the Rabinowitz category of small distribution ranges, small populations and narrow habitat requirements (Table 2). A number are intermediate - with either small populations or narrow habitat ranges, as specified by either soil type/geological formation or altitude or both. However, only a few of these rare species are threatened with extinction by habitat destruction, for example, or because of their extremely limited population size and distribution range (Table 1). Many of the rare species are endemic to a specific region, mountain or centre of endemism due to limited distribution and isolation of the geographical and geological factors. Some occur in only one quarter degree square (Table 1), known from only one locality.

Most of the narrow endemics or near-endemics in *Cineraria* are rare due to specific habitat requirements - either edaphic (restricted to a certain soil type or geological formation) or occurring within a narrow altitudinal range, or both. Restriction in altitude range is probably linked to moisture requirements, as many of the species occur in the mist belt (e.g. *C. cyanomontana* and *C. pulchra*). In addition, many species of *Cineraria* grow amongst rocks, which offer some protection against fire in the afro-montane grassland and also from wind and sun in the harsh alpine or arid environments (such as the Kamiesberg and Little Karoo) in which they occur. The run-off from rocks increases the amount of moisture in the soil at the base, and as noted, moisture availability is a critical factor in the survival of *Cineraria*.

Although certain species of *Cineraria* are not rare, if the infraspecific level is considered, they contain rare subspecies or varieties. For example, *C. lobata* ssp. *lasiocaulis* is known from only a small area in the Karoo; *C. erodioides* var. *tomentosa* is known only from a hillside near Gogogo in Venda; and *C. mazoensis* var. *graniticola* grows only on the granite inselbergs in Zimbabwe. The use of infraspecific categories enables the formal recognition of variation within species, and thereby provides information for conservation of genotypes (Stace, 1976; Snaydon, 1984). In contrast to this viewpoint, Gaston (1994) considers that only species can be considered rare and dismisses lower categories. However, what may be considered distinct species by some taxonomists, may by others be differentiated only at the level of subspecies, yet be as genetically distinct. This problem would be overcome if populations rather than species could be assessed for conservation purposes, as advocated by Rojas (1992). In South Africa, where most of these rare infraspecific categories in *Cineraria* occur, the subspecies and varietal levels are usually regarded to be worthy of attention by conservation bodies at provincial level.

Gaston (1994) also considers that only a low abundance and/or small range size determine whether a species is rare or not. In this, he follows Reveal (1981) who states that “rarity is merely the current status of an extant organism which, by any combination of biological or physical factors, is restricted either in numbers or to an area to a level that is demonstrably less than the majority of other organisms of comparable taxonomic entities”. However, consideration of habitat requirement and availability influences/ determines how likely a species is to be found in localities not yet accounted for - or to move to such areas if a current habitat/location is threatened.

Phylogenetic position may also be a possible cause of rarity - i.e. recently speciated /highly derived species may not have dispersed to their full potential. Unfortunately phylogenetic information is not available as no robust phylogeny for all species of *Cineraria* exists and the molecular (plastid and nuclear) phylogenies for about half the species provide conflicting information.

Origin of Cineraria

Separate molecular and combined molecular and morphological phylogenetic analyses of about half the species in *Cineraria* (Chapters 2 and 3) point to a southern African origin for *Cineraria* in the Western and/or Eastern Cape of South Africa, based on the hypothesis that *Bolandia* is the sister group to *Cineraria*. *Bolandia pedunculosa* occurs in the mountains of the Western Cape, in the southern Drakensberg of the Eastern Cape and at the highest point in southern Africa - on the slopes near the summit of Thaba Ntlenyana in Lesotho. *Bolandia argillacea* is endemic to Brandwag Peak near Worcester in the Western Cape, and also occurs at high altitude. The distribution of *C. mollis* (the species placed sister to the remaining samples of *Cineraria* included in the molecular analyses in the separate and combined ITS analyses) overlaps with that of *Bolandia*, as it occurs in the mountains of the Western and Eastern Cape and extends into Lesotho, the south-eastern corner of the Northern Cape and KwaZulu-Natal on the Drakensberg mountain range.

The paucity of molecular variation in *Cineraria* (Chapter 2) suggests that it is fairly recently evolved. Hybridization has evidently played a major role in speciation in *Cineraria* (Chapters 2 and 3) and it is likely that dispersal has played a major role in determining its current distribution. The colonization of Madagascar by the ancestor of *Cineraria anampoza* provides evidence for long distance dispersal capability as it must have dispersed there from Africa after the separation of Madagascar from mainland Africa in the mid-Cretaceous (Leroy, 1978). Long distance dispersal across continents has also been postulated/recorded for other members of the Asteraceae (Baldwin *et al.*, 1991; Liston & Kadereit, 1995). The current distribution of *Cineraria* in South Africa also suggests that species could have expanded their ranges during wetter periods and retracted in drier phases (Van Zinderen Bakker, 1978; Werger 1983), leaving isolated populations that could have speciated allopatrically.

Conclusion

A variety of factors have therefore influenced the formation of species in *Cineraria*, their current distribution and their rarity. As noted previously, most species of *Cineraria* have very specific habitat requirements - amongst rocks or at the base of cliffs, usually on the south-facing or south-east facing aspects of mountains in the southern hemisphere, indicating that moisture and fire are important determinants of distribution and successful establishment of populations. Its past history, specific edaphic and altitudinal requirements have resulted in a high degree of endemism within the genus and a relatively high proportion (31%) of rare species.

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